THE COMPARATIVE OSTEOLOGY AND SYSTEMATIC STATUS OF THE GEKKONID GENERA AFROEDURA LOVERIDGE AND OEDURA GRAY.

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(Plate viii; eleven Text-figures.)

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Synopsis.

The lizard genus *Afroedura* Loveridge was erected to accommodate those African geckos which were previously included in the Australian genus *Oedura* Gray. Succeeding workers have not always accepted this action, but the present study of the osteology of these two genera confirms their generic status and suggests that they are not closely related.

The use of pupil form in gekkonid classification is shown to be of doubtful validity when applied to living examples of Australian species.

1. INTRODUCTION.

The genus Afroedura was erected by Loveridge (1944) to accommodate those African geckos previously included in the genus Oedura Gray. It has as its type species and subspecies Afroedura karroica bogerti Loveridge.

Since its description *Afroedura* has not found universal acceptance among herpetologists. It has been used by some workers (Mertens, 1954, 1955; Underwood, 1954; Holder, 1960) but not by others (Webb, 1951; Tasman, 1958).

The genus *Oedura* has as its type species *Oedura marmorata* Gray from Australia. Indeed, the Australian members of this genus are remarkably homogeneous, both in their osteology and external morphology, and form one of the most discrete genera of Australian gekkonid lizards.

Although Underwood (1954), largely on the basis of the form of the pupil, placed *Afroedura* and *Oedura* in different subfamilies within the Gekkonidae (Gekkoninae and Diplodactylinae respectively), it appears that doubt still exists as to the taxonomic status of *Afroedura*; however, acceptance or rejection of this genus is of more than minor taxonomic importance. If these two groups of species, one in Africa and the other in Australia, are retained in the one genus *Oedura*, then the implications are of considerable geographic significance. Such a distribution pattern, in which two congeneric species groups were to occur in Australia and southern Africa without any closely allied forms in the intervening area, would be unique among reptiles (and most other groups of terrestrial animals). It was probably with this problem in mind that Darlington (1957) cautiously stated that ". . . *Oedura* is now restricted to numerous Australian species; the related or at least similar *Afroedura* is confined to southern Africa".

In view of these implications, and in the absence of a comparable degree of affinity between any other African and Australian herpetofaunal elements, the osteology of these two groups of gekkonid lizards has been examined in an attempt to establish the order of their relationship.

2. MATERIALS AND METHODS.

Material examined for comparative osteological features included 24 specimens representing all species of the Australian genus Oedura (Cogger, 1957), Afroedura transvaalica platyceps (Hewitt) and Afroedura karroica (Hewitt). Alizarin skeletal

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transparencies were prepared using a technique modified from that outlined by Davis and Gore (1947). All illustrations of skeletal parts were prepared with an eyepiece graticule grid in a binocular dissecting microscope.

3. COMPARISON OF THE GENERA.

Loveridge, in describing his new genus Afroedura, offered the following diagnoses:

Oedura: Four or more pairs of scansors beneath the fourth toe; tail not verticillate. Australia.

Afroedura: One to three pairs of scansors beneath the fourth toe; tail verticillate (not noticeably so in *pondolia*). Southern Africa.

Loveridge proposed the term "scansors" for "... those specialized subdigital scales which have sometimes been referred to as 'adhesive lamellae' or frequently as just 'lamellae', resulting in confusion with the simple lamellae beneath the basal portion of the digit". Such terminology seems to be unnecessarily specialized, as in most geckos there is a wide range of intermediate conditions between the undivided basal lamellae and tubercles and the divided distal lamellae.

Loveridge's diagnoses are generally valid, although occasional specimens of several *Oedura* species are found with only three pairs of lamellae beneath the fourth toe.

The major osteological differences between the two genera are shown in Text-figures 1-11, and are numerated in Table 1.

TABLE	1.
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Oedura.	Afroedura.		
1. Nasals paired.	1. Nasals fused.		
2. Vomers paired.	2. Vomers fused.		
3. Premaxillaries partially fused.	3. Premaxillaries completely fused.		
4. Stapes imperforate.	4. Stapes perforated at its base.		
5. Interclavicle kite-shaped.	5. Interclavicle cruciform.		
 Scapulo-coracoid with minute or absent median coracoidal fenestra. 	 Scapulo-coracoid with very large median coracoidal fenestra. 		
7. No process on the posterior edge of the pleurapophysis of the second sacral vertebra.	7. A large, flattened, triangular process on the posterior edge of the pleurapophysis of the second sacral vertebra.		

Although the degree of fusion between various pairs of cranial elements is known to vary ontogenetically, the adult condition is remarkably constant within any one genus (Camp, 1923; Stephenson & Stephenson, 1956; Stephenson, 1960; Kluge, 1962). Camp (1923) states that the nasals are paired in all gekkonids. Stephenson (1960) found fused nasals in only two of the genera that he examined (*Phyllodactylus marmoratus and Lepidodactylus woodfordi*).

Similarly Camp states that the vomers (= prevomers) are not fused in the geckos. Stephenson (1960) implies that the vomers were paired in all species examined by him.

In view of these findings, the fusion of both the nasals and vomers in *Afroedura* (as was also described by Webb, 1952, for *Afroedura karroica*) would certainly indicate a lack of close affinity between this genus and *Oedura*. Unfortunately no juveniles of any species of *Afroedura* were available to the author, so that it was not possible to determine whether fusion of these cranial elements occurs early or late in the ontogeny of members of this genus.

The other features noted in Table 1 are also known to be relatively stable in any one genus. Holder (1960) noted the occurrence of the large, triangular process on the hind edge of the pleurapophysis of the second sacral vertebra of *Afroedura transvaalica*. She also noted the absence of this process in every endemic Australian gekkonid genus except *Heteronota*, and stated that there was "... no indication ... of a transitional state between the smooth shaft and the shaft with a large process ..." in any of the



Fig. 1. Dorsal aspect of skull of Oedura monilis.



Fig. 2. Dorsal aspect of skull of Afroedura transvoalica platyceps.



Fig. 3. Ventral aspect of skull of Oedura monilis.



Fig. 4. Ventral aspect of skull of Afroedura transvaalica platyceps.

geckos that she examined. This process is extremely well developed in both of the *Afroedura* species examined, but is absent in all Australian *Oedura*.

The extreme difference in shape between the interclavicles of *Oedura* and *Afroedura* is undoubtedly of phyletic significance. The perforation of the columella auris by the stapedial artery, which occurs in only a few living reptiles, is considered by Romer

		TABLE 2.				
Species (Number of Specimens).		Presacrals.	Cervicals Without Ribs.	Lumbar.	Sacral.	Pygal,
O. marmorata (4)		26	3	1	2	4 (5)
0. monilis (4)		26	3	1 (2)	2	5
0. tryoni (1)		26	3	1	2	5
O. robusta (2)		26	3	1	2	5
0. l. lesueurii (11)		26 (25-27)	3 (2-3)	1 (1-2)	2	5 (4-5)
A. transvaalica (1)	• •	27	3	2	2	4
A. karroica (1)	•••	26	3	2	2	5

(1956) to be of considerable phyletic significance. Stephenson (1960) states that the columella is imperforate, presumably in all species examined by him, so that the perforation of the footplate of the columella in *Afroedura* and the imperforate condition in *Oedura* greatly substantiate the view that there is no close affinity between them.

No other differences of major or diagnostic significance were observed, and it should be noted that the expanded clavicle of *Oedura monilis* in Text-figure 7 is not charac-



Fig. 5. Outer aspect (upper) and inner aspect (lower) of mandible of Oedura monilis.

teristic of the genus. Holder (1960) compared the axial skeletons of numerous gekkonid genera, including *Afroedura* and *Oedura*, without noting any significant differences between the two genera except in the structure of the second sacral vertebra (already noted in Table 1). Vertebral counts are given in Table 2. Where they deviate from those observed by the author, Holder's figures are placed in parentheses.

The phalangeal formulae of 2.3.4.5.3 for the manus and 2.3.4.5.4 for the pes are the same in both genera. The carpi and tarsi are also essentially identical in the two genera.

The skeleton of *Afroedura* tends to be relatively more expanded than that of *Oedura*, as shown in the skull and girdles (Text-figs 1, 2, 7, 8, 9 and 10), while the frontal and post-frontal regions of the skull are more elongate in *Oedura*. Although this flattening may be characteristic only of the two species of *Afroedura* examined (*karroica* and



Fig. 6. Outer aspect (upper) and inner aspect (lower) of mandible of Afroedura transvaalica platyceps.

transvaalica), in both of these species the head and body are more depressed than in any species of Oedura.

FitzSimons (1943) states that femoral pores are lacking in all African species of *Oedura* (= *Afroedura*), whereas femoral pores are present in the males of all Australian species of *Oedura* (Cogger, 1957).



Fig. 7. Ventral aspect of pectoral girdle of Oedura monilis.

In the classification proposed by Underwood (1954) the form of the pupil was used as the diagnostic feature separating the Diplodactylinae from the Gekkoninae. The former (in which he included *Oedura*) he defined as "pupil vertical with straight margins, or circular", and the latter (in which he included *Afroedura*) as "*Gekko*-type pupil or secondarily circular". It is interesting to note the extent to which the pupils of living specimens conform to Underwood's findings. The pupil margins of preserved *Oedura* (Plate viii, A) are almost invariably crenate (45 specimens of 5 species examined), yet in all living



Fig. 8. Ventral aspect of pectoral girdle of Afroedura transvaalica platyceps.Fig. 9. Ventral aspect of pelvic girdle of Oedura monilis.

specimens seen by me the pupil is vertical, with straight margins (Plate viii, B). However Bustard (*in litt.*) informs me that Central Australian 0. *marmorata* may have pupils with crenate margins.

While examining pupil shape in various living examples of *Oedura*, and in view of the significance of pupil shape in living diplodactyline species, the pupils of some species



Fig. 10. Ventral aspect of pelvic girdle of Afroedura transvaalica platyceps. Fig. 11. Sacral vertebrae of Oedura monilis (A) and Afroedura transvaalica platyceps (B).

of Diplodactylus were also examined, with interesting results. Although living specimens of Diplodactylus vittatus (Plate viii, D), D. tessellatus (Plate viii, H) and D. steindachneri were found to have the straight-margined vertical pupil described by Underwood, other species of the same genus (D. intermedius, D. williamsi, D. ciliaris and D. taenicauda) were found to have the characteristic gekkonine pupil (Plate viii, E-G) not unlike that of Gekko vittatus (Plate viii, J). It was also found that in those species of *Diplodactylus* with *Gekko*-type pupils, the margins of the latter became smoother as the pupils expanded in poor light, so that in some living *D. elderi*, for example, the pupils were almost straight-edged, whereas in other specimens (Plate viii, I) the margins were clearly crenate. A typical diplodactyline pupil is shown in *Phyllurus platurus* (Plate viii, C).

It is not the author's intention to discuss here the merits of the classification proposed by Underwood; however, it is clear from Plate viii that many living diplodactyline species lack the "straight vertical pupil" described by Underwood, and that a critical re-examination of his diagnostic features is called for.

4. CONCLUSIONS.

The differences between *Oedura* and *Afroedura* are considered by the author to support fully their generic status; indeed, it appears highly probable that similarities between the two genera are the result of convergence, and are not indicative of close affinity.

Earlier assumptions of affinity were founded largely on the arrangement of the subdigital lamellae, a morphological feature on which much of the early classification of geckos was based. Yet even in this character the resemblance between *Oedura* and *Afroedura* is superficial; members of the two genera can generally be distinguished by using the simple diagnoses supplied by Loveridge (1944).

The criteria used by Underwood (1954) in allocating these genera to different subfamilies within the Gekkonidae are of doubtful validity.

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6. ABBREVIATIONS USED IN TEXT-FIGURES.

art, articular; boc, basioccipital; bs, basisphenoid; cl, clavicle; co, coronoid; col, columella auris; dent, dentary; ecpt, ectopterygoid; ep, epipubis; epc, epicoracoid; ept, epipterygoid; exo, exoccipital; fr, frontal; hi, hypoischium; ic, interclavicle; il, ileum; is, ischium; j, jugal; lef, lateral coracoidal fenestra; mcf, median coracoidal fenestra; mx, maxilla; na, nasal; of, obturator foramen; p, pubis; pa, parietal; pal, palatine; pmx, premaxilla; pof, postfrontal; prf, prefrontal; pro, prootic; pt, pterygoid; q, quadrate; sa, surangular; sef, scapulo-coracoid fenestra; sco, scapulo-coracoid; sf, supracoracoid foramen; soc, supraoccipital; sp, splenial; ssc, suprascapula; st, supratemporal; stm, sternum; trc, trabecula communis; vo, vomer; xi, xiphisternum.

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EXPLANATION OF PLATE VIII.

A, Eye of preserved specimen of Oedura l. lesucurii (Duméril & Bibron). B, Eye of living specimen of Oedura l. lesucurii. C, Eye of living specimen of Phyllurus platurus (White). D, Eye of living specimen of Diplodactylus vittatus Gray. E, Eye of living specimen of Diplodactylus intermedius Ogilby. F, Eye of living specimen of Diplodactylus williamsi Kluge. G, Eye of living specimen of Diplodactylus ciliaris Boulenger. H, Eye of living specimen of Diplodactylus elderi Stirling & Zietz. J, Eye of living specimen of Gekko vittatus Houttuyn.